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A Contribution to the Physiology of Tendrils.*

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Entada scandens Benth. is an example of the group of plants which have developed climbing organs from leaves, and which exhibits the transition forms between the initial leaf and the tendril bearing organ.

The genus *Entada* includes five climbing species, some of which have the power of grasping supports by means of the stalks of the pinnae, the others have converted the terminal pair of pinnae into a highly specialized pair of tendrils. *Entada scandens* and *E. polystachys* belong to the latter class.

The adult plant of *E. scandens* consists of a roughened, thick, densely branching vine, which climbs over small trees and shrubs, attaining great distances and heights. In some instances the apex of the principal stem has been found 100 metres from the root.

The leaves are 15–30 cm. in length and consist of a short petiole and an elongated midrib bearing a terminal pair of cylindrical tapering tendrils 5–6 cm. in length. The base of the petiole forms a large pulvinus capable of movements through an angle of about 100 degrees in response to heat and light stimuli. The apical portion of the leaf bearing the tendrils is exposed and the tendrils become active before the pinnules are unfolded. The leaves are generally securely anchored before the green surfaces are de-

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veloped by this arrangement. If a tendril fails to grasp a support it soon dies and is cast away in the same manner as useless leaves or pinnae.

Concerning the history of the development of tendrils on seedlings, Schenk says "Von *Entada scandens* habe ich eine Keimflanze im Bonner Bot. Garten beobachtet. Aus dem dicken grossen Samen kommt ein langer dünner Hauptstengel hervor, dessen erste Blätter keine Spreiten entwickeln, sondern am Ende des Stieles nur je eine Doppelranke tragen. Erst wenn der Stengel einige Fuss hoch ist, folgen auf diese rankenartigen Niederblätter normale gefiederte Blätter mit endstandiger Doppelranke."*

Seedlings grown in a plant house at the University of Minnesota exhibit four or five basal club-shaped bracts attaining a length of 8 or 9 mm. before dropping away. The fifth leaf consisted of a short midrib bearing a pair of irregular stubby pinnae 2 mm. in length, near the base, and a pair of tendrils springing from a point 1 mm. from the tip of the midrib. The basal pinnae bore lateral papillose extensions 8 mm. in length representing pinnules. The tendrils attained a length of 7 mm. and assumed the normal position but were not at any time capable of reaction or of grasping an object. The entire petiole and midrib measured 17 mm. and reached its maturity at a time when the plant stood 19 cm. above the ground. The sixth leaf was furnished with two pairs of lateral branches beside the apical pair of tendrils. In other plants the imperfect tendrils or the branching of the rudimentary rachis did not occur until the sixth leaf had appeared. The leaves successively increased in size and were functionally perfect both as to tendrils and laminae at a varying distance from the base.

Anatomy.

The tendrils are tapering cylindrical, 5–6 cm. in length, when first exposed they adhere by the adjoining surfaces in such manner as to present a D-shaped outline, and do not separate and become irritable until a length of 1.5 or 2 cm. is attained. In the mature tendril the arrangement of tissue is strictly isodiametric. A radius

* Beiträge zur Biol. d. Lianen 1 : 155. 1892.

of the cross section would expend one-sixth of its length in passing the medulla and xylem, two sixths in passing through the phloem and three sixths in the cortex and epidermis. The structure allows great flexibility, rapidity of reaction, and admits of curvature in any direction. A further adaptation to these demands consists in the extremely small size of the cells.

The epidermal cells are rich in protoplasm, the outer walls are markedly outwardly convex, and the three diameters of the cell are nearly equal. The cortical cells impinge directly on the epidermis, and a most notable fact is the entire absence of an external layer of collenchyma. The cortex contains a large amount of chlorophyl and the globoid cells are arranged in six to eight layers with marked intercellular spaces. The inner boundary of the cortex is marked by a sheath consisting of one to three layers of cylindrical parenchymatous cells completely filled with a densely granular substance resembling the gluclosides. Similar cells occur in the phloem and even in the xylem. The medulla is composed of very small elongated cells which have become sclerotized. The tendril then consists mechanically of a cylindrical core of mechanical elements enclosed in a thick cylinder of motor tissue, both of which have a strictly radial symmetry.

IRRITABILITY.

The tendrils appear equally sensitive over their entire length and at a temperature of 33° C. react to contact after a latent period of 5–10 seconds and regain the original position in 10–12 minutes if the contact is but momentary. If a tendril is pressed by means of tweezers or the thumb and finger, no curvature is induced, since the organ is equally stimulated to curve in opposite directions.

When plants growing in the open air are examined, it is difficult to find them in a "normal" or unirritated condition, since they are in a state of rapid circumnutation, are very flexible and easily swayed by the wind; then the contiguity of the two tendrils in a pair allows them to be thrown together very easily. As a result of these facts, the tendrils are generally more or less curved into a hook form, in which condition they will more readily grasp a twig

or other support. The most advantageous position in general would be when the organs are separated with their axis forming an angle of 45 degrees, and the tips curved in any direction except toward the other tendril. If the movements of the leaf should bring a branch between the arms of the Y thus formed, it will be enclosed in 50 to 80 seconds, which is perhaps the most efficient work of any climbing device.

The Sensory Zone.

The sensory zone apparently consists of the single layer of epidermal cells. These cells, seen from the surface, exhibit the greatest diameter tangentially, and seen in cross section the diameters are nearly equal. The nucleus occupies a central position, and the ectoplasmic layer on all sides is extremely thick and very densely granular. It is of course impossible to discover the condition of these elements in an unstimulated condition.

The outward convexity of the external membranes would offer most advantageous conditions for the appreciation of delicate stimuli. The contiguity of the motor cortex cells with numerous interprotoplastic connections would facilitate the transmission of impulses.

Mechanism of Curvature.

The method of production of curvature was determined by measurements of the cortical and epidermal cells of the convex and concave sides of curved tendrils and comparison of the same with data obtained from straight organs. The measurements of one set are given below:

Table I.

Measurements of opposite sides of straight organs.

Number of Cells.		Length.	Average.	Number of Cells.		Length.	Average.
Epidermis	8	797	12.1	Epidermis	9	100	11.1
	5	102	20.4		5	100	20.
	4	96	24.		6	100	16.6
(A)	4	104	26.		4	110	27.5
Epidermis	10	100	10	Epidermis	10	100	10
	7	100	14.3		6	98	16.3
	6	94	15.6		6	100	16.6
(B(	4	94	23.5		4	98	24.5

TABLE II.

Measurements of tendrils stimulated and quickly killed. Sets of cells directly opposite in the same section were measured.

Convex Side Number of Cells.	Length.	Average.	Concave Side Number of Cells.	Length.	Average.
Epidermis 10	100	10	Epidermis 12	100	8.3
8	95	11.9	7	100	14.3
6	100	16.6	8	105	12.5
4	100	25	9	100	11.1
Epidermis 10	100	10.	Epidermis 12	100	8.5
8	105	13.1	8	100	12.5
5	104	20.8	7	108	15.4
5	95	19.	7	100	14.3
3	100	33.	5	100	20.

The average length of the four sets of cells of a straight tendril were 19, 17.8, 14.5, 15.6 with a grand average length of 16.725. The average lengths of the cells from the convex sides were 14.5 and 16.2 with a grand average of 15.15. The average length of the cells from the concave sides of the same tendrils were 11.25 and 13.

It is found, as a result of these measurements, that the cells of the concave side have undergone such diminuition in the longitudinal axis as to measure less than the average normal cells and less than the corresponding cells of the convex side. The cells of the convex side have not increased beyond the average of normal cells. It is evident, therefore, that the curvature of the tendrils is to be ascribed to the action of the cells becoming concave. This action presumably resembles that of the pulvinus of *Mimosa*. Such mechanism is in fact demanded by the structure of the tendril and the rapidity of the curvature necessary to make the motion efficient and economical.

MORPHOLOGICAL CHANGES DUE TO CONTINUED PRESSURE.

The greater portion of the tendril is usually engaged with the support and the free basal portion is rarely a centimeter in length. After the apical portion has engaged the support the basal portion becomes curved in some instances sufficiently to form one complete spiral. In no instance, however, was the arrangement of the

freely curved base sufficient to give an elastic or springing attachment of the leaf which is, in consequence, held in its position quite rigidly.

The portions of the tendril in contact with the support show an increased diameter and a general thickening of the cell walls. The contents of the glucoside cells have nearly disappeared, suggesting that this substance functions as reserve material.

In the outer region of the glucoside cells a ing of libriform tissue is formed which is four or five layers in thickness on the concave side and scarcely half as much on the convex. This ring, as well as the woody, is lignified. The cortex has increased in thickness by simple enlargement of cells. The subepidermal layer has perhaps undergone division forming irregular and much compressed cells. The cells of the epidermal layer of the concave side have undergone enlargement in a radial direction so that this diameter is two or three times as great as the diameter parallel to the surface of the organ. The increase is principally in the form of a greater convexity of the outer wall. The entire concave surface of the tendril has epidermal cells forming irregular papillae, consisting of a group of six to fifty cells. Such an arrangement would fasten the organ quite firmly to the support. The epidermal cells of the convex side have undergone no marked changes except in increase in the axes parallel to the surface and decrease of the convexity of the outer walls.

General Conclusions.

Schenk has pointed out that the theory of Darwin, that all tendril-bearing plants were originally twiners, is at least not applicable to leaf-climbers, and to climbers with tendrils derived from leaves. Leaf-climbers were doubtless derived from species with elongated weak internodes which grow up through the tangles of jungles. The weight of the stem would be supported upon the neighboring plants by means of the leaves and other lateral members. The movement of the surrounding plants by the wind would tend to produce injuries in the supporting members. The development of the power of response to contact would enable the

ancestral climbers to avoid this injury, and at the same time climb more effectively. The development of the irritability to contact in the extremities of the leaf and the transformation of such members into filiform organs would be a natural consequence, and an inevitable one in species bearing large or extended leaves, such as the one under consideration. Furthermore, the general phylogeny of *Entada* would not indicate that it has been a twiner at any time in its existence.

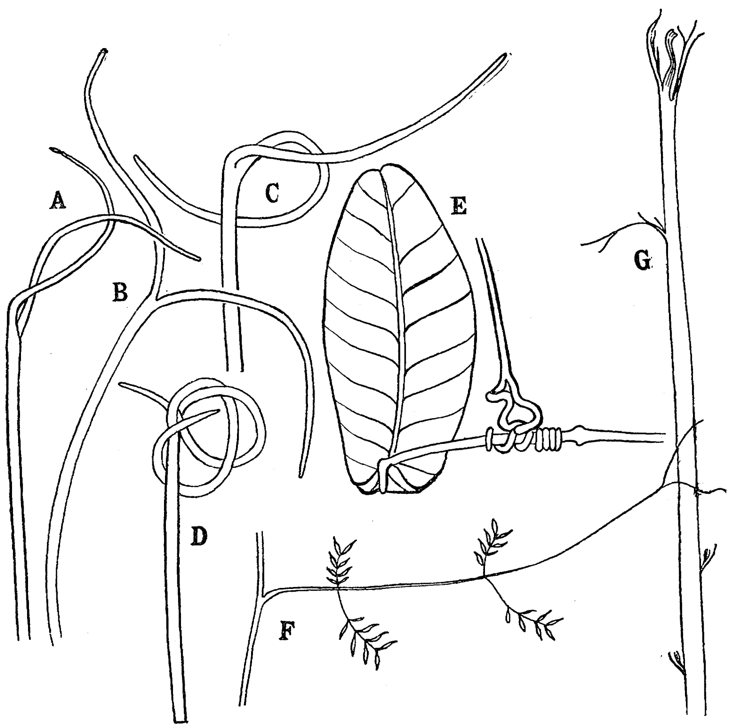
A consideration of the features of the irritability of the tendril leads to the conclusion that the efficiency of the tendril is by no means dependent upon the degree of dorsiventrality exhibited. The isodiametric tendrils of *Entada* are quite as effective in grasping supports and exhibit as great a degree of delicacy of sensorial action as any organs yet examined, and they show no tendency toward dorsiventrality.

Dorsiventrality is induced only by pressure of the support where it is of some benefit in securing a firmer hold. The delicacy of reaction depends more upon centralization and concentration of the woody cylinder, a fact to which I have previously called attention. The lack of collenchyma in the tendrils of *Entada* is probably due to the almost entire absence of torsional strains during the curvature of the tendril. The collenchyma sheath of many tendrils is doubtless to resist the effects of torsional strain. Attention is to be called here to the fact that, in the tendrils of *Entada,* nearly the entire length of the tendril engages the support in a single continuous spiral, and free coiling forms only part of a circle in the basal portion of the organ.

The mechanism of curvature is seen to resemble that of tendrils of *Passiflora* and the roots of *Zea,* in which the mechanical elements are centralized and in which the motor tissue occupies a relatively great portion of the cross section. Curvature is effected by the contraction of the cells of the side becoming concave, a condition demanded by the rapidity of reaction.

The work recorded in this paper was largely performed in or near the botanical gardens at Castleton and Bath in Jamaica, in the summer of 1897, and the writer is indebted to Hon. Wm.

Faucett for the privileges of the gardens, access to collections and much valuable information.



Explanation of Figures.

The tendrils of *Entada scandens* Benth.

A–E, illustrating positions taken by tendrils. A and C, position resulting from mutual stimulation and nutation. B, normal or unstimulated tendrils. D, curvatures produced by filaments of spider's web. E, tendril attached to leafy branch of supporting plant. F, compound leaf with terminal pinnae converted into tendrils. G, shoot of seedling. The fifth leaf exhibits a terminal pair of tendrils and a single pair of foliar pinnae.